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Ecological commonalities among pelagic fishes: comparison of freshwater ciscoes and marine herring and sprat

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Abstract Systematic comparisons of the ecology between functionally similar fish species from freshwater and marine aquatic systems are surprisingly rare. Here, we discuss commonalities and differences in evolutionary history, population genetics, reproduction and life history, ecological interactions, behavioural ecology and physiological ecology of temperate and Arctic freshwater coregonids (vendace and ciscoes, *Coregonus* spp.) and marine clupeids (herring, *Clupea harengus*, and sprat, *Sprattus sprattus*). We further elucidate potential effects of climate warming on these groups of fish based on the ecological

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Introduction

Fishes are the most diverse group of vertebrates, and almost all aquatic systems (apart from ground-water) support their populations. They have developed an astonishing variety of life styles, feeding modes, morphological adaptations and physiological specializations. However, a major distinction seems to exist between fishes living in freshwater and those living in marine environments. This distinction is less a biological reality and more a difference in the traditional conceptualisation by the researchers who work within these two different aquatic habitats. This division has likely arisen and continues to be supported by the physical separation of working groups between marine and freshwater research institutes, which prevents continued exchange of ideas and fruitful collaborations across aquatic borders. Our contribution aims to bridge this

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division by explicitly comparing groups of fish residing in either of these two main aquatic habitats to find commonalities and fundamental differences. By merging teams of freshwater and marine researchers, the aim of this synthetic work is to identify research gaps and future topics common across aquatic habitats.

We focus on dominant pelagic planktivores, the coregonids in freshwater lakes and the clupeids in marine and brackish waters. Both groups of fish are of high importance to commercial and recreational fisheries (Nyberg et al. 2001; Stockwell et al. 2009; Geffen 2009; Dickey-Collas et al. 2010). We refer in particular to the temperate, boreal and Arctic zones, with a comparison between freshwater ciscoes (*Coregonus* spp.) living in lakes, and the Baltic and North Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). We give more examples for the species of the European temperate zone, because the authors' long research history on these groups facilitates a detailed understanding of the ecology and evolution of these fishes. We explicitly add reference and comparison to Siberian and North-American coregonids for some patterns or processes, but do not cover the species from these geographical areas with similar detail. The emerging reason for our comparison, to be demonstrated by this review, is a surprisingly high number of biological features that are shared by coregonids and clupeids, not least a similar morphology and coloration (Fig. 1). We start by reviewing results on evolutionary history and population genetics to elucidate the local variability of the focal fish groups. We continue reviewing reproduction and life history, ecological interactions, behavioural ecology and physiological ecology. Finally, we elucidate potential effects of climate change on both groups of fish, thus mirroring the general theme of the AQUASHIFT priority program (see this Special Issue of Marine Biology for more examples). Generally, we start by discussing aspects of the biology of coregonids and then report on similar aspects of clupeids. We close each part by a summary, in which we explicitly compare the two groups and suggest future research topics.

Evolutionary history and population genetics

In the European temperate and boreal zones, only a few species of pelagic planktivorous coregonids can be found. Especially in deep lakes with a low number of other competing fish species, coregonid populations are known to segregate in their niches, mainly by specializations to either littoral, pelagic or profundal habitats. Ecological segregation is often observed for populations of whitefish (*Coregonus lavaretus*) (Østbye et al. 2005; Kottelat and Freyhof 2007; Hudson et al. 2011; Kahilainen et al. 2011b). Typically, a smaller planktivorous form residing in the

pelagic area lives sympatrically with one or two larger benthivorous forms found in littoral or profundal zones (Siwertsson et al. 2010). However, because usually only one morph is strictly pelagic, we do not consider populations of *C. lavaretus* in more detail here.

The other widely distributed European pelagic *Coregonus* species is vendace (*Coregonus albula*) (Fig. 1) that is common in deep, oligo- to mesotrophic lakes of Scandinavia and northern Germany, Poland and Russia (Kottelat and Freyhof 2007; Mehner et al. 2007a). Vendace spawn in late autumn in most of the lakes. In a few lakes of Scandinavia, Russia and Germany, spring-spawning ciscoes are found, primarily sympatric with vendace. Lake-endemic spring-spawning species with viable populations are *C. lucinensis* (Fig. 1) from Lake Breiter Luzin (Germany) (Thienemann 1933), *C. fontanae* from Lake Stechlin (Germany) (Schulz and Freyhof 2003), *C. trybomi* from Lake Fegen (Sweden) (Svårdson 1979) and *C. kiletz* and *C. ladogae* from Lakes Onega and Ladoga (Russia), respectively (Pravdin 1936). Similar spring-spawning species usually referred to as *C. trybomi* have existed or still exist in some lakes of Finland and Karelia (Airaksinen 1968) and may have gone extinct in three other Swedish lakes (Kottelat and Freyhof 2007).

Studies on genetic differentiation between these populations of sympatric and allopatric ciscoes are rare. By studying enzyme gene variability of Finnish populations, Vuorinen et al. (1981) concluded that autumn-, winter- and spring-spawning populations do not form monophyletic units. More detailed genetic analyses by using a range of marker sets revealed a complex phylogeographical history of the German sympatric populations (Schulz et al. 2006; Mehner et al. 2010b). Spring-spawning ciscoes were genetically most closely related, but formed a separate cluster together with their sympatric vendace populations relative to other allopatric vendace populations. This pattern suggests the potential of parallel sympatric speciation in both lakes, but the genetic signature modified by secondary contacts and partial hybridization with other *Coregonus* lineages (Mehner et al. 2010b). Furthermore, there was a significant isolation-by-distance pattern in the genetic differentiation between German vendace populations (Mehner et al. 2009). Therefore, partial isolation and local adaptation in the often small lakes contribute to the evolutionary history of *Coregonus* populations despite the relatively short time since last glaciation.

Well-defined cisco species from Siberia and Northwest America encompass least cisco (*Coregonus sardinella*), Bering cisco (*C. laurettae*) and Arctic cisco (*C. autumnalis*) (Turgeon and Bernatchez 2003; Politov et al. 2004), the latter also occurring in Ireland (Harrod et al. 2001). Only *C. sardinella* are primarily living in lakes, whereas *C. laurettae* and *C. autumnalis* are anadromous (Brown et al.



Fig. 1 Photographs of a number of coregonids and clupeids discussed in this paper. From top to bottom *Coregonus albula* (Lake Breiter Luzin, 120 mm total length (TL), picture: Jörg Freyhof); *Coregonus artedi* (Lake Superior, 386 mm TL, picture: Gary Cholwek); *Coregonus lucinensis* (Lake Breiter Luzin, 122 mm TL,

picture: Jörg Freyhof); *Coregonus hoyi* (Lake Superior, 212 mm TL, picture: Zach Woiak); *Clupea harengus* (Western Baltic, 285 mm TL, picture: Sophie Bodenstein); *Sprattus sprattus* (Bornholm basin of Baltic Sea, 123 mm, picture: Holger Haslob)

156 2007), and *C. atumnales* phenotypically resemble more the
157 European whitefishes than ciscoes (Kottelat and Freyhof
158 2007). A centre of coregonid diversity in North America are
159 the Laurentian Great Lakes, with eight species recognized
160 (Scott and Crossman 1973; Todd and Smith 1992) from
161 which longjaw cisco (*C. alpenae*) and deepwater cisco
162 (*C. johannaes*) have gone extinct. Four of the other six species
163 (*C. zenithicus*, *C. reighardi*, *C. kiyi*, *C. nigrispinnis*) are
164 threatened or vulnerable, whereas only bloater (*C. hoyi*) and
165 lake herring (*C. artedi*) (Fig. 1) occur in abundant popula-
166 tions. Recent analyses by mitochondrial and microsatellites

markers elucidated that genetic variation between the cisco
populations in the Great Lakes reflected geography rather
than taxonomy, and hence, it was recommended that a single
taxon (*C. artedi sensu lato*) be recognized, covering all cisco
species in the Great Lakes (Reed et al. 1998; Turgeon et al.
1999; Turgeon and Bernatchez 2003). In the Great
Slave Lake (NT, Canada), *C. artedi*, *C. zenithicus* and
C. sardinella coexist (Vecsei et al. 2011).

The mechanisms and strength of genetic differentiation
between populations differ between freshwater and
marine fishes because marine environments present fewer

geographical barriers to dispersal and higher levels of connectivity. Accordingly, effective population sizes are large resulting in limited genetic drift, and hence, low levels of genetic population structure are common among marine fish species (DeWoody and Avise 2000; Puebla 2009). Surprisingly, few studies exist on cases of ecological divergence and sympatric speciation in marine fishes similar to those often observed in the more isolated freshwater systems (Puebla 2009), although local adaptation and limited dispersal cannot be excluded to be important also in marine systems (Jørgensen et al. 2008).

The Atlantic herring (*Clupea harengus*) (Fig. 1) might be a good example. This species exhibits a complex population structure with several divergent populations referred to as subspecies, stocks or groups (Iles and Sinclair 1982; McQuinn 1997a). Significant, albeit weak, genetic differentiation has been found between local stocks (Larsson et al. 2010), but the greatest differences were detected between the highly saline North Sea and the brackish Baltic Sea subpopulations (Bekkevold et al. 2005; Ruzzante et al. 2006; Larsson et al. 2007). A striking similarity to coregonids is the variation of spawning times of herring populations, with spawning peaks in spring, autumn and winter all occurring in the Atlantic and the adjacent North and Baltic Seas. In the Western Baltic, spring- and winter spawning, populations of herring locally coexist (Bekkevold et al. 2007). The herring stocks from the Northwest Atlantic can be divided into northern and southern groups and have different spawning times. The northern group is found from the Gulf of St Lawrence to the south coast of Greenland and spawns in spring. The southern population occupies the area south of the Gulf of St Lawrence to the Virginia coast and spawns in autumn (Klinkhardt 1996; Stephenson et al. 2009).

Genetic analyses by microsatellites revealed two different processes by which winter spawning may have arisen from the otherwise dominant spring-spawning mode. In one population from inner Danish waters, a founder effect from a distant winter-spawning population was likely. In contrast, 'spawning time switching' (McQuinn 1997b) from spring to winter spawning has been suggested for the herring population close to the island of Rügen (Germany), as suggested by low differentiation between spring- and winter spawners (Bekkevold et al. 2007).

No genetic differences between spawning populations have been found for sprat (*Sprattus sprattus*) (Fig. 1), the other common pelagic clupeid in European temperate marine ecosystems (Limborg et al. 2009). This is in part surprising because sprat show distinctly separate spawning grounds in the Baltic Sea (Arkona, Bornholm and Gotland basins) as well as seasonally changing circulation patterns, which could provide regionally self-sustaining populations.

Similarly, no significant genetic differentiation exists between North Sea and Baltic Sea populations of sprat (Debes et al. 2008). In contrast, strong genetic differentiation exists between Atlantic and Mediterranean or Black Sea stocks, coinciding with different temperature preferences of the respective populations with subspecies recognized (Debes et al. 2008).

Summary and comparison

Evolutionary significant units can be found in both coregonids and clupeids of the temperate and Arctic zones that are considered valid species in European, Siberian and Northwest American coregonids (Turgeon and Bernatchez 2003; Kottelat and Freyhof 2007), discrete phenotypes of one lineage (*C. artedii*) as the result of incipient processes of parallel diversification in the Great Lakes (Turgeon and Bernatchez 2003), and subspecies or stocks in clupeids (McQuinn 1997a). Among the coregonids, genetic differentiation is primarily driven by geographical distance. If different lineages came into secondary contact after last glaciation, introgression and hybridization promoted adaptive radiations along ecological gradients (Turgeon and Bernatchez 2003; Mehner et al. 2010b). If combined with allochrony of spawning times, populations in geographically isolated lakes split into discrete species (*C. fontanae* of Lake Stechlin, *C. lucinensis* of Lake Breiter Luzin) (Mehner et al. 2010b). In contrast, genetic differentiation remained weak in less-isolated systems where the populations still show overlapping spawning times (*C. artedii* sensu lato of the Great Lakes).

The situation is less clear for clupeids where the populations show only weak genetic differentiation, and where genetic exchange between the stocks is likely due to dispersal and straying into various reproductive areas from populations that coexist at feeding grounds (McQuinn 1997a; Gaggiotti et al. 2009). Therefore, the Atlantic herring stocks are considered to form a meta-population (McQuinn 1997a). Furthermore, there is no clear correspondence between spawning time and genetical identity, because both 'spawning-time switching' within populations and founder effects from extant populations have been shown to form local populations with deviating spawning times (Bekkevold et al. 2007). Only the latter process may produce genetical distinctness between spring- and autumn spawners and hence can be assumed to facilitate local adaptive ecological divergence similar to the processes known for coexisting spring- and autumn-spawning coregonids.

Overall, the pelagic fish species covered in this review mirror the gradient of ecological speciation typically found in fishes (Hendry 2009). Systems vary from continuous adaptive variation without reproductive isolation in the

clupeids, over discontinuous adaptive variation with minor reproductive isolation in the Great Lakes ciscoes, to adaptive differences with reversible reproductive isolation in the sympatric European ciscoes and the allopatric Siberian and Northwest American ciscoes. Recent evidence for hybrids between vendace and European whitefish (Kahilainen et al. 2011a) supports that irreversible reproductive isolation has not yet been achieved in these post-glacial diversifications of species.

Reproduction and life history

Despite its broad distribution range, comparative overviews on the life history and reproduction of vendace are rare. Vendace is a relatively small, short-lived species with a plastic life history strategy (Bøhn et al. 2004; Gregersen et al. 2011). Maximum length and age are reported to be 25–30 cm and 5–7 years, respectively, in the majority of lakes (Schultz 1992; Bøhn et al. 2004), although fish older than 10 years have been found in single lakes (Salonen 2004). Age at maturation is between 2 and 5 years, with males usually reproducing earlier than females (Sandlund 1992; Bøhn et al. 2004). An increased investment into spawning in cold years with low zooplankton abundance has recently been demonstrated (Gregersen et al. 2011). Spawning occurs along the shores, usually in 4–10 m depth, but spawning depth can vary between 1 and 20 m with shallowest spawning observed in the most humic lakes (Heikinheimo et al. 2006). Eggs sink to the bottom. Vendace spawn between early autumn and early winter (late October to November in Scandinavia, December in Northeast Germany) at water temperatures of ca. 6–7 °C (Koho et al. 1991; Nyberg et al. 2001). Larvae hatch in early spring a few days after ice-off in the lakes and spend the first 4–6 weeks close to surface, primarily inhabiting littoral areas (Karjalainen 1992; Nyberg et al. 2001; Karjalainen et al. 2002; Urpanen et al. 2005). This is assumed the most critical phase due to the limited habitat extension and hence high density of larvae. Juveniles of 20–30 mm length move into the pelagic zone and continue to be strictly pelagic over their lifetime. It has to be noted, however, that in some lakes, vendace larvae are exclusively pelagic already immediately after hatch (Karjalainen et al. 2002). An early nearshore phase and migration to deeper areas at about 15–20 mm fish length has been documented also for larval *Coregonus artedii* (summarized by Stockwell et al. 2009).

Year-class strength (YCS) of mature coregonids can vary up to 20-fold (Helminen et al. 1993; Helminen and Sarvala 1997; Nyberg et al. 2001; Stockwell et al. 2009), whereas even higher inter-annual variation has been documented for densities of young-of-the-year (yoy) fish

(Mehner et al. 2011a). Recruitment success of vendace is only moderately proportional to the size of the spawning stock (Helminen et al. 1997; Karjalainen et al. 2000). The abundances of spawners and recruits are best characterized by a compensatory relationship (Valtonen and Marjomäki 1988; Marjomäki 2004). In contrast, larval density at age of 3 weeks and YCS of mature fish are strongly correlated, indicating that the critical period occurs during the first weeks after hatching (Viljanen 1988; Huusko and Sutela 1998; Karjalainen et al. 2000; Marjomäki et al. 2004). Large-scale synchrony in population abundances of coregonids suggests that there is an important density-independent mechanism influencing recruitment (Marjomäki et al. 2004; Bunnell et al. 2010), most likely driven by the temperature development during winter and early spring and date of ice break (Nyberg et al. 2001; Mehner et al. 2011a).

There is little information available on the life history of sympatric coregonids in European lakes (subsequently referred to as ciscoes, including *C. fontanae*, *C. lucinensis* and *C. trybomi*). These species are characterized by spawning in spring and early summer, with the spawning time extending from late April until July (Table 1). *C. fontanae* is smaller than the sympatric vendace in Lake Stechlin (maximum length about 15 cm) (Anwand et al. 1997), whereas *C. lucinensis* (Scharf et al. 2008) and *C. trybomi* are presumably only slightly smaller than vendace. Hatching dates and ecology and distribution of early life stages are widely unknown for these species. Adults of spring-spawning species are pelagic and co-occur locally with vendace where sympatric, but may display vertical segregation from vendace (Mehner et al. 2010a). Among the ciscoes from the Great Lakes, only the allopatric *C. artedii* population of the Lac des Écorces (Quebec, Canada) is a spring-spawner that hatches in later July and has low size after first summer and matures at age 3 (Henault and Fortin 1989, 1993). The other ciscoes of the Great Lakes and Siberia are autumn to winter spawners with comparable maximum size or age, and age at maturation, as found for vendace (Table 1). Interestingly, *C. reighardi* was originally described as spring-spawning species, but a switch towards autumn spawning has been reported in the Great Lakes (Scott and Crossman 1973).

The life history of clupeids in temperate marine systems is well studied. Sprat is a batch spawner and exhibit high spawning activity in different months depending upon the latitude. At the lower latitudinal limit in the Mediterranean (Adriatic) Sea, sprat generally spawns during the winter months (October to April) with peak spawning in November and December at water temperatures between 9 and 14 °C (Dulcic 1998). At the northern latitudinal limit, sprat spawns between March and August in the Baltic Sea (Elwertowski 1960; Parmanne et al. 1994; Baumann et al.

Table 1 Overview on maximum length (L_{\max} , cm), maximum age (A_{\max} , years), age at maturity (A_{mat} , years), spawning months and dominant diet for temperate and arctic freshwater coregonids inhabiting lakes, and for marine clupeids

Species	L_{\max} (cm)	A_{\max} (y)	A_{mat} (y)	Spawning months	Diet
Coregonids					
<i>Coregonus albula</i>	25 (43)	6 (19)	2 (5)	Oct–Dec	Planktonic
<i>Coregonus fontanae</i>	15	3	2	Apr–Jul	Planktonic
<i>Coregonus lucinensis</i>	20	6	2	Apr–Jul	Planktonic/benthic
<i>Coregonus trybomi</i>	20	?	?	Apr–May	?
<i>Coregonus artedi</i>	25 (47)	7 (17)	3 (6)	Nov–Dec	Planktonic
<i>Coregonus hoyi</i>	25 (38)	7 (12)	3–4	Dec–Mar	Planktonic/benthic
<i>Coregonus kiyi</i>	25 (35)	7 (10)	3–4	Oct–Dec	Benthic
<i>Coregonus zenithicus</i>	28 (43)	(11)	4–6	Sep–Nov	Benthic
<i>Coregonus reighardi</i>	25 (36)	(8)	?	Oct–Nov (May ^a)	Benthic
<i>Coregonus nigripinnis</i>	33 (39)	(14)	4–5	Sep–Jan	Benthic
<i>Coregonus sardinella</i>	23 (47)	11 (22)	3 (7)	Sep–Nov	Planktonic/benthic
Clupeids					
<i>Clupea harengus</i>	30 (45)	15 (22)	3 (6)	Jan–Dec	Planktonic
<i>Sprattus sprattus</i>	12 (16)	5 (20)	2	Feb–Jul	Planktonic

Average values are given together with maximum reported values (in parentheses) where available. Data were compiled primarily from taxonomic handbooks (Scott and Crossman 1973; Kottelat and Freyhof 2007) and online sources (www.fishbase.org)

^a *C. reighardi* was considered a spring-spawner according to earlier descriptions (Scott and Crossman 1973)

2006a) and a bit later (May through August) in the North Sea (Wahl and Alheit 1988). Observations in the Baltic detected spawning females as early as January (Haslob et al. 2011), and in 2003, a second spawning peak was observed in autumn, both related to exceptional inflow events of warm North Sea water penetrating deep basins such as the Bornholm Basin (Kraus et al. 2004). Another possible explanation for this second spawning peak is the fact that sprat are able to extend their spawning period by directly channelling energy from food consumption into reproduction and not only relying on the energy stored until maturation (Blaxter and Hunter 1982).

In the Baltic, sprat spawning primarily occurs within deep basins, but occurs in both coastal and offshore waters in the North Sea (Whitehead 1985) and the time of peak spawning, relative fecundity and batch fecundity vary significantly between years and regions (Wahl and Alheit 1988). Batch fecundity is positively correlated with water temperature during the pre-spawning period (Haslob et al. 2011). Salinity changes during the spawning season can modify the buoyancy of the eggs and yolk sac larvae (Petereit et al. 2009). Higher salinity at fertilization increases the specific gravity of eggs and therefore induces a deeper vertical distribution. The resulting variability in vertical distribution can affect the mortality of the sprat eggs by altered temperature and oxygen conditions (Petereit et al. 2008) and a changing overlap of predators and prey. Model simulations by Hinrichsen et al. (2005) have shown that larvae drift to the nearshore juvenile nursery grounds on the Swedish or Polish coastline. The drift

depends on wind direction and forcing thus leading to a mixing of the juveniles from the different spawning stocks. Adult sprat are generally mature at 2 year though some members of the population may spawn at 1 year (Bailey 1982). After the spawning season in the Baltic, adults of sprat leave the deep basins to feed in shallower, coastal waters. Age-0 juveniles join adult schools in the autumn and re-emigrate with adults to the spawning grounds in late winter. In the North Sea, the spawning and migration dynamics of sprat as well as herring can be considered a marine estuarine opportunist strategy (Thiel and Potter 2001; Guelinckx et al. 2006).

Atlantic herring spawns in coastal and shelf regions across the northern Atlantic Ocean while its sister species (Pacific herring, *Clupea pallasii*) spawns in similar habitats throughout the northern Pacific. Atlantic herring displays remarkable flexibility in its spawning phenology utilizing every season depending upon the specific ecosystem such as summer (northern Baltic), spring (Norway), autumn (northern North Sea) and winter (southern North Sea) (see Hufnagl and Peck 2011, their Fig. 7). In the North Sea, four different stocks (Shetland/Orkney, Buchan, Banks, Downs) have been described, which differ in growth rates, migration routes (Harden Jones 1968) and recruitment patterns (Dickey-Collas et al. 2010). In the North Sea, herring show anti-clockwise migration patterns with the fish leaving the overwintering grounds in the eastern North Sea (Norwegian coast) to move westwards to the feeding grounds. Spawning starts on the east coast of Scotland in August/September and continues to September/October for

the herring spawning in the Dogger Bank area. October to January is the spawning time for the Downs and Channel herring (Harden Jones 1968; Blaxter and Hunter 1982). Once entrained as juveniles to a spawning ground by joining migrating adults, the majority of the spawning group returns to the same grounds from year to year (homing) (Stephenson et al. 2009).

In the eastern North Sea, the Norwegian Sea, the Skagerrak and the Baltic Sea, spawning primarily takes place in spring, but with smaller autumn- and winter-spawning population components occurring locally (Blaxter and Hunter 1982). Spring spawners also are more abundant in the western Atlantic herring stocks in colder waters where the larvae have to grow during summer to reach the juvenile stage in late summer or autumn. Autumn spawners in the western Atlantic are found in southern areas where larvae spent a longer time in colder winter waters before they reach metamorphosis in spring. This represents two strategies to cope with different environments during early development of the offspring (Messieh 1975; Melvin et al. 2009). In the northwest Atlantic, herring utilizes spawning areas from Labrador to Cape Hatteras (Messieh 1988; Safford and Booke 1992; Armstrong and Cadrin 2001).

Autumn spawners mostly deposit eggs on specific spawning grounds in deeper offshore areas, whereas spring-spawning herring utilize shallow near-coast habitats (Klinkhardt 1996). As opposed to sprat, herring are single-batch spawners spawning only one batch per year in schools with the composition of the school changing over time, since individuals appear and disappear from the spawning ground (Blaxter and Hunter 1982; Axelsen et al. 2000; Skaret et al. 2003; Geffen 2009). Individual females leave the school, deposit their “sticky” demersal eggs mainly on plant material (like *Fucus*, *Laminaria*, *Zostera*) on the sea floor in the Baltic and mainly on gravel and rock and mussel beds in the North Sea (Geffen 2009) and are followed by one or more males which fertilize the newly spawned eggs (Aneer 1982). After spawning, there is a mixing in the central North Sea when the fish migrate easterly to the overwintering grounds near the Norwegian coast and the Skagerrak. Cushing (1975) modified the “triangle of migration” (Harden Jones 1968) by including the early life stages and linking their larval drift patterns to circulation features.

Herring show a very flexible life history strategy with embryos and larvae from these different herring stocks experiencing different salinities, temperatures and day lengths as well as predator fields and food availabilities on their spawning grounds (Klinkhardt 1996; Geffen 2009). The composition of mesozooplankton communities in the Baltic Sea changes regionally due to differences in ambient salinity and temperature (Möllmann et al. 2000).

Thus, herring and their offspring will be faced with different food sources in the different spawning regions (Möllmann et al. 2005). Autumn and winter spawners have larger eggs than spring and summer spawners (Blaxter and Hempel 1963; van Damme et al. 2009). The eggs of the spring spawners are larger than those of the summer spawners, a strategy used to compensate for the greater variability in the production cycle during the spring-spawning phase (Blaxter and Hunter 1982). Survival of the offspring in autumn/winter in a season of low productivity is possible, since herring larvae are able to survive long periods of little or no growth and the larger size of the larvae affects their survival chance (Johannessen et al. 2000; Geffen 2009).

Summary and comparison

The life histories of coregonids and clupeids are strikingly similar with both groups maturing early in life, having low to moderate longevity and maximum sizes not exceeding about 30–35 cm (Table 1). Likewise, both groups often utilize nearshore areas for spawning, the eggs of coregonids and herring are attached to substrates or sink to the shallow bottom, and the early larvae can occur in shallow nearshore areas. The benefit from this benthic spawning strategy is that growth of the larvae occurs in a very specific region at a very specific time without large dispersal losses after long incubation periods (Blaxter and Hunter 1982). After the nearshore phase, older larvae leave their initial feeding habitat, and either migrate over short (freshwater coregonids) or passively drift long (marine clupeids) horizontal distances to their pelagic habitats where they spend the juvenile and adult phases before returning to the nearshore habitats for spawning. Baltic sprat are an exception in that they also utilize offshore, deeper areas for spawning with larval drift to shallower areas.

Another important characteristic for both groups is that a high variety of spawning times (from autumn over winter to spring and early summer) are utilized by distinct populations (particularly herring and ciscoes) and that spawning-times appear to have evolved as an adaptation to intense competition and local conditions at the spawning grounds (in both groups) or within larval/juvenile nursery areas (in clupeids) (Gaggiotti et al. 2009). A systematic understanding of the correspondence between spawning time, spawning duration, fecundity and egg size, larval mortality and the abiotic conditions at the spawning location (temperature, salinity) might be a promising research avenue within the framework of the plasticity of life history strategies in fishes. This approach could benefit from an explicit comparison of coregonids and clupeids.

549 **Inter- and intraspecific ecological interactions**

550 Coexisting populations of coregonids have repeatedly been
 551 used as model organisms to study competitive interactions
 552 within the process of ecological speciation (Østbye et al.
 553 2006; Bernatchez et al. 2010; Siwertsson et al. 2010). Most
 554 of these populations follow the typical benthic-pelagic
 555 segregation, but other types of ecological divergence are
 556 also found (reviewed by Hudson et al. 2007). Ecological
 557 segregation along the depth gradient within the pelagic area
 558 is less frequently reported than the benthic-pelagic diver-
 559 gence, but is nevertheless described in a few lakes.
 560 Examples include ciscoes in Lake Nipigon, North America
 561 (Turgeon et al. 1999), and coexisting vendace and white-
 562 fish in Lake Skrukkebukka, northern Norway (Gjelland
 563 et al. 2007).

564 Vendace has a high number of gill rakers and is regarded
 565 a specialist zooplanktivore (Hamrin 1983; Viljanen 1983;
 566 Northcote and Hammar 2006), although recent observa-
 567 tions suggest some flexibility in diet choice (Liso et al.
 568 2011). Due to its efficient zooplankton foraging, vendace
 569 may outcompete and hence exclude other planktivorous
 570 fish species from the pelagic area (Beier 2001; Bøhn and
 571 Amundsen 2001) and cause changes in the zooplankton
 572 community (Karjalainen and Viljanen 1993; Helminen and
 573 Sarvala 1997; Amundsen et al. 2009). A strong influence of
 574 planktivory on the zooplankton community has also been
 575 found for *C. artedi* (Rudstam et al. 1993). Inter-cohort food
 576 competition in vendace populations is strong, in particular
 577 during the warmer summer months, and hence, population
 578 dynamics of vendace in many lakes is characterized by bi-
 579 annual cycles (Hamrin and Persson 1986; Helminen et al.
 580 1993; Helminen and Sarvala 1994; Karjalainen et al. 2000).

581 A recent comparison of several lakes (Kahilainen et al.
 582 2011b) illustrated that the predation efficiency for zoo-
 583 plankton increased with the number of coregonid (vendace
 584 and whitefish) forms that coexist in a lake. Along this
 585 gradient of planktivore efficiency, the zooplankton com-
 586 munities were modified accordingly, resulting in smaller-
 587 sized prey in the lakes containing the most efficient
 588 planktivorous forms with highest number of gill rakers
 589 (Kahilainen et al. 2011b). In contrast, for sparsely rakered
 590 forms, this reduction in prey size has probably reduced the
 591 opportunity to utilize the zooplanktivorous niche in these
 592 lakes. As a result of this eco-evolutionary feedback
 593 between predators and prey, the formation of intermediate
 594 phenotypes has decreased and resource segregation among
 595 the coregonids increased (Kahilainen et al. 2011b). In this
 596 context, almost nothing is known on the competitive
 597 strength of the spring-spawning *Coregonus* species. In
 598 Lake Stechlin, both vendace and Fontane cisco are truly
 599 pelagic and utilize the same planktonic food source
 600 (Helland et al. 2008), suggesting strong exploitative

601 competition. Similar feeding efficiencies for zooplankton
 602 in vendace and Fontane cisco from Lake Stechlin
 603 (Ohlberger et al. 2008a) suggest no advantage of vendace
 604 over cisco in exploiting pelagic zooplankton resources.

605 Competition and niche partitioning between the
 606 North-American ciscoes in the Great Lakes have not been
 607 thoroughly studied, but recently Gamble et al. (2011a)
 608 simulated a food web of the pelagic fish community in
 609 Lake Superior. This study showed that the dominant
 610 planktivores in the lake are cisco (*C. artedi*) and kiyi
 611 (*C. kiyi*). Additionally, a third coregonid species, bloater
 612 (*C. hoyi*), also inhabits the pelagic area. In spite of some
 613 seasonal variations, the three species appear to largely
 614 overlap in diet, with *Mysis* as the most important prey,
 615 similar to the dominance of *Mysis* in the diet of *C. lucinensis*
 616 in the German Lake Breiter Luzin (Scharf et al. 2008). Yet,
 617 cisco has a more flexible diet compared to the other species
 618 which includes more calanoid copepods, *Daphnia* and
 619 *Bythotrephes* (Gamble et al. 2011a). This is probably rela-
 620 ted to the fact that cisco also exhibits more variation in the
 621 seasonal diel migration than the other coregonids. Another
 622 recent study examined trophic niche partitioning among all
 623 deepwater coregonids in the Great Lakes, based on stable
 624 isotopes of both historical and contemporary data (Schmidt
 625 et al. 2011). These results indicate that within all lakes,
 626 individual species have occupied distinct ecological niches.
 627 The ecological distinctness has been dynamic, but yet
 628 maintained over time in spite of ecological disturbances.
 629 The study suggests that segregation in habitat depth seems
 630 to be the major driver of the niche divergence among
 631 coregonids in the Laurentian Great Lakes.

632 Great Slave Lake, Canada, consists of several coregonid
 633 populations that have remained more intact compared to
 634 those in the Laurentian Great Lakes, thanks to fewer
 635 human-induced changes. Also here the taxonomy is not
 636 resolved, and the ecological diversity is not well described.
 637 It seems, as if the lacustrine cisco (*C. artedi*) might have
 638 overlapping diet or habitat with some of the other forms
 639 in the pelagic area (Muir et al. 2011). In Barrow Lake,
 640 Canada, cisco is reported to coexist with shortjaw cisco
 641 (*C. zenithicus*). Shortjaw cisco mainly eats *Mysis*, and only
 642 limited amounts of copepods and cladocerans (Steinhilber
 643 et al. 2002).

644 Also in marine environments, pelagic clupeids are
 645 known to influence zooplankton dynamics, which conse-
 646 quently regulate competitive interactions among planktiv-
 647 orous fishes. For example, variations in herring condition
 648 have been explained by plankton availability, partly regu-
 649 lated by both intraspecific (density-dependence) and
 650 interspecific competition with sprat (Möllmann et al. 2005;
 651 Casini et al. 2010). Sprat is a strict zooplanktivorous spe-
 652 cialist, while herring may feed upon zooplankton and
 653 benthic food organisms as large juveniles and adults.

Hence, the interspecific competition between sprat and herring is likely strongest at smaller size (Casini et al. 2004). However, the diet overlap between herring and sprat does not only change ontogenetically, but also varies seasonally and with prey abundance and composition (Casini et al. 2004).

As mentioned above, ecological divergence and local adaptations seem to be highly important in both freshwater coregonids and marine clupeids, and in both systems genetically distinct spawning populations likely have resulted, at least in part, from competitive interactions. However, while comparisons of sympatric populations of coregonids mostly have focused on variation in feeding habitat resulting from competition among adults, studies of sympatric herring populations have mainly described variation in spawning behaviour, probably related to competition between younger stages. Although a comprehensive mechanistic understanding has not yet been achieved, it has been proposed that competition for a suitable substratum for eggs and for food among larvae could be involved in the spawning time divergence in herring (Jørgensen et al. 2005).

A similar competition among younger life stages may have been important in the development of the segregated spawning periods between the coregonids in Lake Stechlin (Helland et al. 2008, 2009). Although adults of vendace and Fontane cisco show only subtle ecological differences, their larvae most likely share much less ecological similarities. Because the larvae of the two species hatch at different times of the year, autumn- and spring spawners probably face highly dissimilar environments (e.g. temperature, predation risk, food abundance) during their first weeks of life (Nyberg et al. 2001). Development of reproductive isolation in sympatry cannot happen without simultaneous reduction in the competition, to allow the divergent populations to coexist (Coyne and Orr 2004). Asynchrony in timing of spawning and hatching may contribute directly to the coexistence of sympatric populations, through temporal partitioning of resources and habitat.

Predatory interactions are functionally similar for coregonids and clupeids. Substantial mortality of coregonids is found during the larval phase, primarily induced by perch (*Perca fluviatilis*) predation (Helminen and Sarvala 1994; Huusko et al. 1996). Juvenile and adult coregonids are important prey items of the few pelagic piscivores, such as perch, brown trout (*Salmo trutta*) or lake trout (*Salvelinus namaycush*) (Heikinheimo 2001; Valkeajärvi and Marjomäki 2004; Hrabik et al. 2006; Gamble et al. 2011a, b).

Cod is the main predator on sprat and herring in the Baltic Sea (Sparholt 1994). It could be shown that sprat and herring stocks substantially benefited from the decreased predation pressure imposed by cod and from concurrently

low rates of fishing mortality (Köster et al. 2003). In the Baltic Sea, predation on eggs of herring and sprat is temporally variable and seems to depend upon the extent of vertical overlap between adults and eggs (Köster and Möllmann 2000a, b). Sprat larvae were only occasionally discovered in low numbers in the stomachs of clupeid (herring and sprat) predators, suggesting low predation mortality of larvae by clupeids (Köster and Möllmann 1997). The feeding impact of medusae and chaetognaths on fish early life history stages in the Baltic is also very low (Barz and Hirche 2005). Another predator for sprat in the Baltic are piscivorous seabirds, for example the common guillemot *Uria aalge* that directly affects the sprat population in the Baltic and is indirectly affected by the fishery strategies on sprat and cod (Österblom et al. 2006).

In marine systems, herring and sprat form important trophodynamic links between lower (zooplankton) and upper (piscivores) trophic levels. In different regions, the populations of both sprat and herring exhibit out of phase oscillations with populations of their key predators suggesting strong top-down control. Examples of this tight coupling between populations of sprat and herring and those of gadoid predators include sprat and Atlantic cod (*Gadus morhua*) in the Baltic Sea and herring and haddock (*Melanogrammus aeglefinus*) on Georges Bank in the northwest Atlantic (Richardson et al. 2011). Although heavily exploited in fisheries, multispecies virtual population analyses suggest that removal of these clupeids by predators exceeds that by commercial fisheries (Tyrrell et al. 2008).

Similarities between coregonids and clupeids can be found also with respect to host–parasite interactions. The dominant parasites of coregonids are cestodes, primarily transmitted via copepods that are part of the planktonic diet of coregonids (Hoff et al. 1997; Pulkkinen et al. 1999; Pulkkinen and Valtonen 1999). In Atlantic herring, 41 marine parasite species including metacercaria, nematodes and gastrointestinal trematodes were found (Arthur and Arai 1984; MacKenzie 1987). Transmission of most of these parasites seems to be restricted to the coastal waters. Tolonen and Karlsbakk (2003) studying the parasitic assemblage in Norwegian spring-spawning herring found very similar assembly as in other North Atlantic fish stocks. In Baltic herring, 31 parasitic species have been recorded and 23 species in the North Sea (MacKenzie 1987). Parasitic infestation with the larvae of *Anisakis simplex* (nematode) was shown for sprat and herring in the Baltic Sea varying significantly with geographical region. Highest infection rates were found in areas of low salinity, low temperature and reduced oxygen conditions. Sprat was less affected than herring (Grygiel 1999) indicating differences in susceptibility to diseases between herring and sprat. Endoparasitic infections with metacercaria, larval

nematodes and larval cestodes in herring were analysed for their use in stock identifications. The study showed a remarkable stability in the parasite fauna over time and showed a significant difference in the prevalence and infection of the parasite infracommunities validating the use of parasites as biological tags and as a method for stock discrimination (Campbell et al. 2007).

In the North Sea, herring larvae are known to suffer mortality due to both endo- and ectoparasites including nematodes and cestodes, and certain copepod species, respectively (Rosenthal 1967). Heath and Nicoll (1991) reported that larvae infected by the cestode (*Scolex pleuronectis*) had nearly a 50 % reduction in feeding incidence (24 %) compared to those that did not contain endoparasites (44 %). Furthermore, no larvae smaller than 15 mm contained these endoparasites, whereas incidences of infection increased with increasing body size in larvae >15 mm and were highest in coastal waters. Those authors speculated that this biological mechanism may interact with changes in drift trajectories to affect YCS of herring in the North Sea. More recent work (Lusseau et al. 2009) utilized the prevalence of endoparasites as an index of larval feeding incidence, overwinter survival and YCS.

Summary and comparison

In both clupeids and coregonids, planktivory is the dominant feeding strategy, although single populations may show locally deviating strategies with an enhanced uptake of benthic animals or even fish. However, a complete switch to benthivory, as often observed in one of the coexisting freshwater whitefish populations, has been documented only in the deepwater forms of *C. artedii* s.l. of the Great Lakes (Table 1). Therefore, there is a fixed connection of niche dimensions between pelagic habitat use and planktonic feeding strategy. The dominant planktivory may intensify intra- and interspecific competition because there is no further specialization and niche segregation possible (in contrast to the variety of benthivorous or piscivorous feeding strategies). This limited niche segregation along the diet axis in the pelagic habitat may contribute to forced microhabitat segregation along the depth and temperature gradients as found in pelagic coregonids. However, it may also explain why divergent selection operates primarily on the early life stages in both groups. The result, spawning-time switching, might be the most efficient strategy to reduce competition by avoidance of simultaneous occurrence of comparable life history stages and similar-sized individuals. The primarily pelagic life style of coregonids and clupeids also results in predator–prey and host–parasite interactions that are functionally comparable. There is growing evidence that these ecological interactions likewise contribute to local adaptation of

populations (Fraser et al. 2011). However, these interactions and their correspondence to ecology and life history of the species are much better studied in the marine than in the freshwater species.

Behavioural ecology

Diel vertical migration (DVM), one of the most striking patterns of rhythmic population behaviour, has been repeatedly documented from planktivorous coregonids. The regular DVM consists of the occurrence of fish in relatively dark and cold hypolimnetic areas during daytime, an ascent into warmer metalimnetic waters during dusk, a night-time occurrence in metalimnetic waters, and a descent back into deep layers during dawn. DVM in coregonids has been reported from several lakes (Dembinski 1971; Hamrin 1986; Hrabik et al. 2006; Stockwell et al. 2010). Ascent and descent are proximately triggered by the change of illumination threshold during dusk and dawn (Jurvelius and Marjomäki 2008; Busch and Mehner 2009). The ultimate causes of coregonid DVM have been widely discussed with some controversy, but most researchers suggest that fish leave the well-lit near-surface layers during daytime to avoid visually oriented predators (Hrabik et al. 2006; Gjelland et al. 2009). Interestingly, however, evidence for high predation risk of coregonids in shallower layers of lakes could rarely be found, because the density of piscivores was in most cases surprisingly low (Hrabik et al. 2006; Stockwell et al. 2010; Mehner et al. 2010a). Therefore, a genetically fixed migration has been discussed as a response to the ‘ghost of predation past’ (Mehner et al. 2007b; Jurvelius and Marjomäki 2008).

An additional ultimate cause of DVM was put forward for the coregonids of Lake Stechlin, where hydroacoustic observations of population depths at night revealed strong seasonal fluctuations, with fish occurring in deeper water in spring and autumn than during the summer months (Mehner et al. 2005, 2007b). There was a significant correlation between population depths and vertical temperature gradients (Mehner et al. 2007b; Busch and Mehner 2009), suggesting that fish seek layers with metabolically optimum temperatures at night (Mehner et al. 2010a). However, a bioenergetics benefit of DVM for Lake Stechlin coregonids could not be demonstrated. Busch et al. (2011) used a bioenergetics model to explore that the regular DVM is not the most efficient strategy. They suggested that multiple factors, rather than bioenergetics efficiency alone, are the evolutionary basis to explain DVM. In addition, no growth advantage (that should be expected when bioenergetics efficiency is assumed to drive DVM) was found for vendace switching in experiments between high and low temperatures relative to fish held at constant

temperatures (Mehner et al. 2011c). However, fish performing DVM may benefit from predation avoidance without compromising their metabolic balance and hence growth rates (Mehner et al. 2011c).

Regular DVM is also well described from populations of Atlantic herring and sprat in the North and Baltic Seas (Nilsson et al. 2003; Cardinale et al. 2003; Axenrot et al. 2004; Orłowski 2005). The utilization of DVM by sprat in the Baltic appears to have changed in the last decade. Previously (in the 1990s), sprat larvae in the Bornholm Basin performed a normal DVM, being captured during the day in deeper water layers (e.g. below the thermocline, 40 m) and at night in surface waters. In contrast, a consistent lack of DVM was observed when sprat were re-sampled in the same system from 2002 to 2005 (Voss et al. 2007). The lack of DVM in recent years is hypothesized to be due to changes in the abundance of copepod species that have different depth preferences. Specifically, the abundances of *Acartia* and *Temora* species which prefer warmer, surface waters have increased, whereas the abundance of *Pseudocalanus* which inhabits deeper, colder, more saline depths has decreased (Voss et al. 2007). Biophysical modelling results of larval feeding and growth that included these decadal changes in prey fields and water temperatures suggested fitness benefits related to the change in larval DVM behaviour (Hinrichsen et al. 2010). Modelled larvae that maintained the originally normal DVM in recent years could not meet energy requirements due to the poor foraging environment at depth.

A variety of mechanisms have been proposed to modify DVM of herring larvae such as hydrographic characteristics (mixed or stratified water body), tidal influences (Stephenson and Power 1988), the combination of light and turbulence (Heath et al. 1988), dependency of light and food availability (Munk et al. 1989) and predator–prey relationships (Bailey and Houde 1989; Houde 1989). For North Sea herring, Heath et al. (1991) and Haslob et al. (2009) observed that herring larvae had a distinct vertical migration to upper water layers during the day and more homogenous depth distribution during the night with larger larvae showing a more pronounced behaviour. The size-dependent vertical distribution pattern of the herring appears to be due to the vertical distribution of their prey organisms (Munk et al. 1989). Since herring larvae are visual predators that cannot feed at low light intensities (Blaxter 1962), they have to swim to the upper water layers to be able to feed, a behaviour that will be influenced by the degree of mixing or stratification present within the water column. During the summer in deep Baltic basins, the adults of both sprat and herring perform DVM with fish moving towards surface layers (upper 20 m) at dusk and back to daytime depths of 60–80 m at dawn (Stepputtis 2006).

Reverse migration patterns with an ascent into shallower layers during dawn and a descent during dusk have recently been documented for young-of-year herring in a brackish bay of the Baltic Sea (Jensen et al. 2011). Furthermore, the vertical distribution at midday was bimodal, suggesting two alternative migration strategies in these small herring, somehow similar to a pattern found in coregonids in Lake Stechlin (Mehner and Kasprzak 2011). Similar to the larval sprat example, the change in DVM pattern was consistent with bioenergetics-based predictions of net energy gain. In the case of herring, the occurrence in warmer water during the daytime facilitated rapid digestion at intense feeding phase, whereas herring do not feed at night and hence save energy by descending into colder layers (Jensen et al. 2011). These bioenergetics-based explanations of behavioural patterns are expanded upon in the next section.

Summary and comparison

Diel vertical migrations are common behavioural strategies in both coregonids and clupeids. This commonality suggests that the vertical gradients of the pelagic habitats in both freshwater and marine ecosystems create comparable selective forces on habitat-choice behaviour. The primary gradients triggering DVM seem to be illumination strength as the proximate factor, and temperature that may be considered as both proximate (guiding the fish into preferred habitats) (Levy 1990) and ultimate (fitness advantage at increased bioenergetics efficiency of growth) (Brett 1971) factor. However, vertical distributions of prey, intra- and interspecific competitors, and predators are locally variable, and hence, a single unique evolutionary causation of DVM across all populations and habitats cannot be achieved. In turn, this variety of local conditions may explain why DVM patterns have been found to be both seasonally and annually highly variable in some of the studied populations and may respond to drastic change in environmental factors (Hinrichsen et al. 2010). The individual variability within population-wide migration patterns and its evolutionary causation has just started to be explored (Mehner and Kasprzak 2011). During early ontogeny, physostome fishes such as clupeids and coregonids must ascend to surface waters and gulp air to fill their swim bladders. Thus, ontogenetic changes in depth distribution are also related to this functional, morphological constraint (Blaxter and Batty 1984).

Physiological ecology

Abiotic gradients contribute to the structuring of freshwater and marine fish assemblages. Factors of major interest are temperature and oxygen, and additionally salinity in

marine ecosystems. Ecological specialization along these gradients in response to strong competition involving traits not related to feeding strategies has been discussed to contribute to speciation in fishes (Mehner et al. 2011b). Often, these traits are directly or indirectly related to spawning time and location, thermal habitat use and energetic trade-offs.

Vendace and Fontane cisco in Lake Stechlin display an ecological and physiological segregation with respect to water depth and thermal habitats, which is as well associated with differences in spawning time. The sister species show differences in metabolic rates with respect to temperature (Ohlberger et al. 2008b) and thermal preferences (Ohlberger et al. 2008c) that correspond to the ecological divergence in habitat use (Helland et al. 2007, 2008) and suggest different energetic strategies. Ohlberger et al. (2012) demonstrated that the scaling of metabolic rate with body mass is temperature-dependent in both vendace and Fontane cisco in contrast to other species. This intra-specific temperature dependence of metabolic rates most likely represents a plastic response of energy metabolism to the changing thermal conditions and suggests a more pronounced competitive superiority of small compared to large individuals at lower temperatures. Differences in size-dependent competition may thus be related to the species' thermal habitats (Ohlberger et al. 2012). Ciscoes in the Great Lakes occupy different water depths and can be grouped into pelagic (*C. artedi*, in part *C. hoyi*) and deepwater phenotypes (*C. kiyi*, *C. zenithicus*, *C. reighardi*, *C. nigripinnis*), corresponding to their primary diet (Table 1). The adaptive diversification of the deep-water ciscoes is associated with different physiological abilities to occupy different water depths, which has been related to body size, mass-specific metabolic rates and buoyancy characteristics (Clemens and Crawford 2009).

Thermal windows supporting the survival of embryos in the laboratory as well as threshold (warm and cold) temperatures avoided by adults in the field have been investigated in coregonids (Dembinski 1971; Crowder and Crawford 1984; Hamrin 1986; Tapaninen et al. 1998) and clupeids (Reid et al. 1996; Peck et al. 2012) (Fig. 2). Embryos of coregonids such as *C. clupeaformis* and *C. albula* can tolerate colder temperatures but have more narrow thermal windows compared to both the embryos of both clupeids considered in this review (sprat and herring). Adult clupeids can exploit a wider range of water temperatures and can grow well at warmer temperatures than adult coregonids. Preferred temperatures often coincide with those optimal for growth (e.g. Jobling 1981), but this depends heavily upon the acclimation characteristics of specific populations (e.g. Pörtner and Peck 2010). Temperatures preferred by juvenile (P^*)

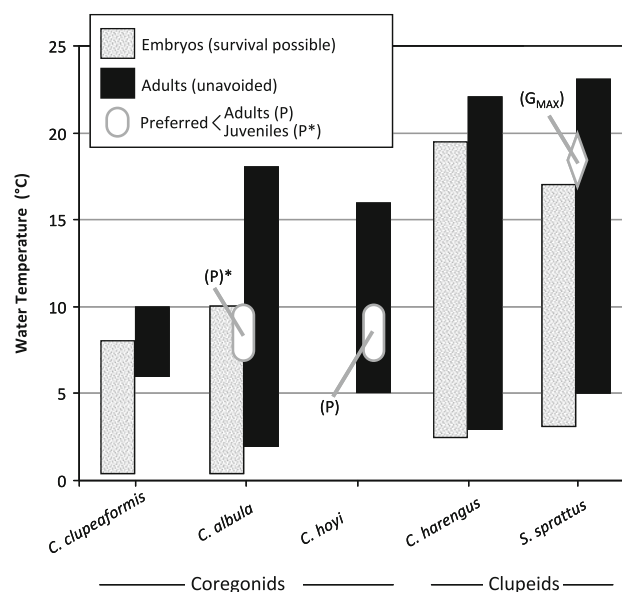


Fig. 2 Thermal windows supporting the survival of embryos in the laboratory as well as threshold (warm and cold) temperatures avoided by adults in the field for three species of coregonids and two species of clupeid fishes. The range in temperatures preferred by juvenile or adult coregonids and that corresponding to maximum growth (in sprat) are also indicated. Data sources are listed in the text

C. albula and adult (P) *C. hoyi* (8–10 °C) are half those at which sprat juveniles obtained maximum growth rates (G_{MAX}) in the laboratory and field (Peck et al., unpubl. manuscript) (see Fig. 2). This brief review of the thermal constraints of *Coregonus* congeners and clupeids (sprat and herring) reinforces the notion that the life stages of coregonids are more constrained to colder water habitats compared to these clupeids but that both groups display ontogenetic expansion of thermal habitat during the late larval/early juvenile phase and have similar thermal ecologies at spawning (e.g. preferred/optimum at 8–12 °C).

Both clupeids tolerate a wide range of salinities and hence are both abundant in brackish waters of the Baltic Sea and marine waters of the North Atlantic. The transition zone between the North Sea and the Baltic Sea is an area with a strong salinity gradient spanning from 30 to 34 ‰ in the North Sea to 6–8 ‰ in the Baltic proper, with levels decreasing even down to 3 ‰ in the innermost (north-eastern) parts of the Baltic (Gaggiotti et al. 2009). Thus, changes in salinity levels may shape fish growth rates both indirectly by changing the zooplankton community structure and abundance and/or directly via effects on growth physiology and metabolism (Cardinale et al. 2002). It appears likely that adaptation to the varying salinity at the spawning location contributes to ecological divergence between herring populations, but there are no physiological studies to support this hypothesis.

1043 Summary and comparison

1044 The study of metabolic divergence of coexisting pelagic
 1045 populations requires further investigations, because tem-
 1046 perature seems to be important for vertical micro-habitat
 1047 segregation, bioenergetics efficiency of growth, body size
 1048 and life history. It would be promising to explore whether
 1049 temperature conditions during spawning season and at
 1050 spawning location, egg size, growth rate, size at maturation,
 1051 maximum size, optimum metabolic temperature and
 1052 final temperature preferendum correspond across the
 1053 coregonid and clupeid populations of the temperate zone.
 1054 This would suggest a functional interaction between life
 1055 history, metabolism and environmental conditions, as
 1056 recently proposed (Killen et al. 2010).

1057 Potential effects of climate change

1058 Studies addressing the effects of global climate change on
 1059 coregonids in lakes are relatively rare (Magnuson et al.
 1060 1990; Elliott and Bell 2011). It is generally assumed that
 1061 the thermal guild of cold-water stenothermal fish to which
 1062 coregonids belong is most vulnerable to global warming
 1063 (Graham and Harrod 2009). This assumption is primarily
 1064 based on the predicted decline of suitable habitats for
 1065 coregonids in lakes due to warming and de-oxygenation of
 1066 deeper water layers (Jacobson et al. 2010; Elliott and Bell
 1067 2011). Nyberg et al. (2001) discussed that the YCS of
 1068 autumn-spawning coregonids whose larvae hatch in early
 1069 spring is expected to decline with warming, whereas the
 1070 YCS of spring spawners might increase because the later-
 1071 hatching larvae of spring spawners can more precisely
 1072 match the temporally shifting peak of zooplankton prey in
 1073 late spring. The coexisting coregonid species in Lake
 1074 Stechlin were an appropriate study system to test this
 1075 assumption. In contrast to the prediction, densities of
 1076 young-of-the-year vendace in June were higher after warm
 1077 winters. However, metalimnetic temperatures in June
 1078 affected densities of juvenile and adult vendace and Fontane
 1079 cisco in opposite direction. Cisco densities were
 1080 higher in warm years, whereas high vendace densities were
 1081 primarily found when June temperatures were cold.
 1082 Metalimnetic temperatures seem to modify the competition
 1083 strength between the interacting coregonids, because high
 1084 densities of cisco forced vendace to occupy shallower and
 1085 hence warmer waters at night, whereas high vendace
 1086 densities forced cisco to stay deeper and hence in too cold
 1087 water (Mehner et al. 2011a).

1088 By using a coupled lake physics and bioenergetics
 1089 model, growth rates of vendace and Fontane cisco were
 1090 simulated for a predicted global change scenario in the year
 1091 2100 (Busch et al. 2012). Two behavioural strategies were

distinguished, with coregonids either performing behavioural thermoregulation (keeping their temperatures at night constant), or fish performing migrations with fixed amplitudes (keeping their depth at night and hence illumination threshold constant). In almost all simulations, coregonids were predicted to increase their growth rates, even by assuming that zooplankton densities might decline by about 10 %. The reason for this unexpected outcome is the opposed temperature development of hypolimnetic and metalimnetic water layers in Lake Stechlin predicted for the warming scenario. Whereas epi- and metalimnetic layers between 0 and 18 m will warm, layers deeper than 20 m will cool down by up to one degree. Accordingly, fish will experience colder water during their daytime residence that reduce their metabolic expenditures, and the energy saved will more than balance the slightly reduced feeding rates from the lower prey densities. However, if fish would follow behavioural thermoregulation under these warming conditions and keep their currently observed temperatures at night, their vertical microhabitat segregation will completely collapse because layers with preferred temperatures for vendace and cisco will then largely overlap. Accordingly, temperature development of the main habitats is coupled with biotic interaction strength, a pattern that has only recently emerged as a main research area (Kordas et al. 2011).

Clupeid fish have been one of the best bio-indicators of climate-driven changes in marine systems, exhibiting strong changes in stock size and distribution because of their short lifespan and tight coupling to zooplankton dynamics and mesoscale hydrodynamic features sensitive to physical forcing (Lluch-Belda et al. 1992; Alheit et al. 2005; Tourre et al. 2007). Similar to the climate discussion of coregonids in lakes, climate change will affect sprat and herring (and other marine fish) in both direct and indirect ways. Direct effects include changes in water temperature, causing species-specific impacts due to differences in thermal windows supporting growth and survival (Pörtner and Peck 2010). Sprat occurs at the northern boundary of its geographical distribution in both the Baltic and North Seas suggesting that additional warming (when considered in isolation of other factors) would benefit these populations (MacKenzie and Köster 2004). On the other hand, at its lower latitude limit, sprat has shown dramatic declines in recent decades such as the disappearance of the spawning population in the Northwest Mediterranean (Calvo et al. 2011). These changes are consistent with the inter-stock, dome-shaped relationship between recruitment and water temperature experienced during spawning (MacKenzie and Köster 2004). Herring, which occurs with sprat at the lower latitudinal extent of its range in the North and Baltic Sea, will also likely experience losses in the productivity of specific spawning stocks in southern regions due to climate warming (as discussed below).

Compared to lake systems, climate change may have potentially more complex impacts in open marine systems due to losses in connectivity between key habitats. Many marine fish, including clupeids, have evolved complex life history strategies that help promote philopatry, habitat connectivity, life cycle closure and population persistence (Harden Jones 1968; Sinclair 1988). Herring displays spawning site fidelity, an adaptive strategy that has likely evolved to place progeny within environments providing favourable transport to areas promoting high rates of feeding, growth and survival during early life (Cushing 1975). Sprat also displays specific preferences for spawning areas such as deep Baltic Basins and the German Bight in the southern North Sea. The YCS of sprat, herring and other marine clupeids has been correlated to atmospheric climate oscillations such as in the North Atlantic (NAO) and Pacific (PDO) (Gröger et al. 2010). These oscillations are not only highly correlated to changes in water temperature but also the strength and direction of regional wind fields causing changes in the drift trajectories of early life stages (Peck et al. 2009), potentially disrupting the connectivity between essential habitats. In the Baltic, sprat year-class strength has been strongly and significantly correlated to the spawning stock biomass and a drift index (Baumann et al. 2006b) with high year classes resulting when larvae are retained near spawning grounds. Recent biophysical modelling work on sprat in the North Sea comparing different NAO years predicted very little change in potential larval survival; despite differences in drift trajectories and water temperatures North Sea sprat larvae matched well (spatially and temporally) with modelled prey fields (Daewel et al. 2008).

In North Sea herring, year-class success of autumn spawners appears to be regulated by processes acting during the early life, as larvae drift from western spawning grounds to eastern juvenile nursery areas (Nash and Dickey-Collas 2005). Using a physiology-based foraging and growth model constructed for larval herring, Hufnagl and Peck (2011) estimated the ability for herring to switch spawning times (or spawning areas) in response to climate-driven changes in key factors (temperature, prey fields). The model suggested that climate-driven changes in bottom-up factors will affect spring- and autumn-spawned herring larvae in different ways. It is unlikely that autumn-spawning herring will be able to avoid unfavourable conditions by delaying their spawning time or by utilizing more northern spawning grounds because of limitations in day-length to larval growth and survival. Conversely, for spring spawners, the success of earlier or later spawning will be tightly constrained by match–mismatch dynamics between larvae and their zooplankton prey (Hufnagl and Peck 2011).

Summary and comparison

Climate warming may affect both fish groups comparably. The most sensitive ontogenetic stages seem to be the fish larvae because of their exposed nearshore habitats in which changes in temperature will occur more pronouncedly than in the much larger pelagic volumes of lakes and seas (see Mehner 2000). Furthermore, volumetric densities of larvae are highest, their daily food demand is highest during ontogeny, and their ability to detect and avoid predators is poorly developed (Houde 1987; Mehner and Thiel 1999; Bochsansky et al. 2008). Therefore, abiotic and biotic factors at nearshore habitats that respond to global warming will have the strongest effect on year-class strengths of coregonids and clupeids, in particular because early life stages have narrower thermal windows than juvenile or adult fish (Pörtner and Peck 2010). For the marine clupeids, the passive transport of late larvae to their juvenile habitats over large distances might be another important phase that can presumably be neglected in coregonids due to the immediate connection of nearshore and pelagic habitats in lakes. Given the potential decline of suitable thermal habitats and limited dispersal opportunity, coregonids in lakes will face changes in competitive interactions and competition strength with changes in the thermal regime (Mehner et al. 2011a).

Because warming may modify autumn, winter and spring seasons differently, the variability of spawning times will cause a response that is specific to each population. In this context, spring-spawning herring seem to be more robust against warming, a pattern that was predicted also for freshwater spring spawners relative to the more vulnerable autumn spawners (Nyberg et al. 2001). A systematic comparison of locally coexisting populations with non-overlapping spawning times could be therefore a promising approach to achieve mechanistic understanding of the most important factors that make pelagic fish populations sensitive to global change.

Conclusions

Our review has explored commonalities and differences in pelagic fish species inhabiting either freshwater or estuarine and marine systems. The potential effects of global change on populations of these fishes will arise from changes in either indirect (trophodynamic) or direct (abiotic, physiological) factors. The severity of impacts will depend to some extent on whether species have the capacity and speed to adapt to these changes via behavioural modification and phenotypic selection.

However, the interplay between genetic differentiation, spatiotemporal distribution, ecological interactions, life

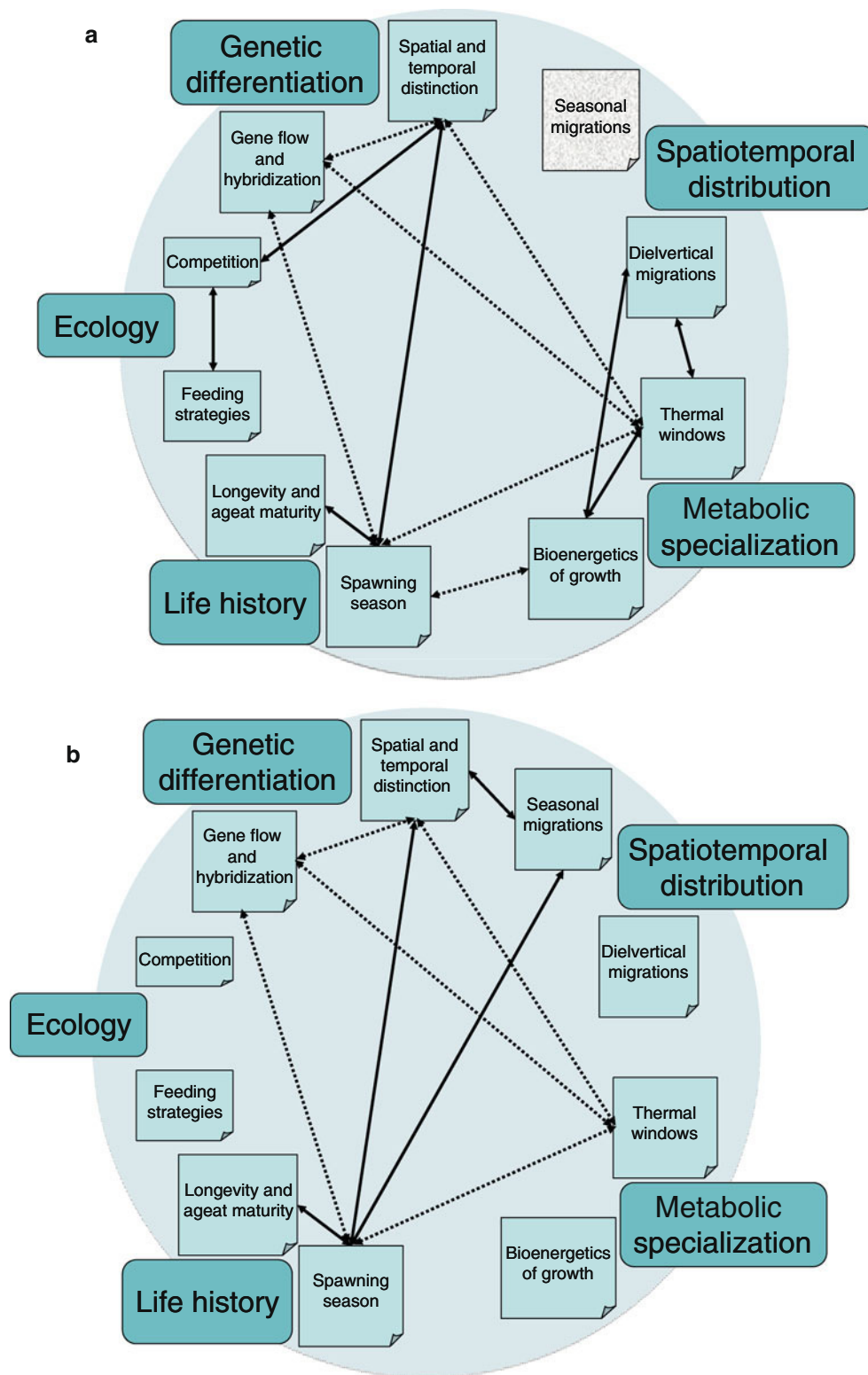


Fig. 3 Conceptual graphics showing the interplay of processes related to genetic differentiation, spatiotemporal distribution, metabolic specialization, life history and ecology of coregonids (a) and clupeids (b). *Solid arrows* indicate good scientific understanding of

links. *Stippled arrows* indicate links that are suggested to be studied in the next years. Seasonal migrations are not described in coregonids, and hence, this box is coloured in grey

history and metabolic specialization has differing research deficits in clupeids and coregonids (Fig. 3). Whereas in coregonids, the interaction of thermal windows and bioenergetics with habitat choice and vertical migrations is well understood (Fig. 3a), these effects are less explored in clupeids. Clupeids show large-scale migrations between reproductive and feeding areas, and individual homing and straying is likely important for genetical population differentiation (Fig. 3b). In contrast, the spatial and temporal organization of spawning in coregonids is not really understood, in particular for the rare spring-spawning species.

A central research theme for both groups can be found in the interplay between life history and physiological specialization, and the resulting genetical differentiation by ecological divergence (Fig. 3a, b). Furthermore, the effect of host–parasite interactions on local adaptation in this context is not understood. It will be important to study whether hybrids between species or populations that differ in spawning season are fertile, and whether they display additive genetic effects with respect to the thermal windows of their parental populations. This may offer insight into the processes that enforce speciation, for example through fitness disadvantages of hybrids relative to their parents. It cannot be excluded that hybridization between metabolically specialized parents is a possible outcome of effects of global warming, for example by induction of temporal overlap of previously distinct spawning times, or habitat temperatures intermediate between those currently dominating in the native habitats.

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